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ULTRASTRUCTURE OF RECTAL PAPILLAE IN THE MALE *DACUS DORSALIS* HENDEL (DIPTERA: TEPHRITIDAE)[1]

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Wen-Yung Lee, Yu-Bing Hwang and Jui-Chun Chang (1992) Ultrastructure of rectal papillae in the male *Dacus dorsalis* Hendel (Diptera: Tephritidae). *Bull. Inst. Zool., Academia Sinica* **31**(3): 181-197. The ultrastructure of rectal papillae in *Dacus dorsalis* Hendel has been investigated by SEM and TEM. Many structures of rectal papillae in this fly are similar to other advanced dipterans; for example, in the rectal papillae of the cortical epithelium and the medulla, there is an infundibular space between these two structures. The cortical epithelium of *D. dorsalis* papillae is covered by a fibrous basement membrane in the basal region, and by a cuticular intima in the apical region. The cytoplasm of the cortical epithelial cells provides many membranous stacks which are associated with the mitochondria which are part of the mitochondrial pump (or ion pump) used for water and ion uptake. In the basal part of the cortical epithelial cells, the basement membrane appears as an amorphous structure; there are many infoldings under this basement membrane which are for ions returning to the cells from the infundibulum. Intercellular junctions were observed; many intercellular spaces penetrate and are scattered throughout the cortical epithelium. Some large intercellular spaces contain two or three tracheoles. The medulla is located at the center of the papillae with a network structure, and is surrounded with medullary cells which are covered by three layers of the basement membrane. The mechanism and route of fluid movement from the rectal lumen to the haemolymph are discussed.

Key words: *Dacus dorsalis*, Rectal papilla, Ultrastructure, Cortical epithelium, Medulla, Mitochondrial pump (ion pump).

The rectal papillae and rectal pads in the hind guts of insects have a special function in the transporting of water and ions from the gut lumen to haemolymph (Wigglesworth, 1932; Berridge, 1967; Smith, 1968; Phillips, 1970; Ramsay, 1971; Berridge and Oschman, 1972; Wall and Oschman, 1975; Noirot and Noirot-Timothee, 1976; 1977).

The ultrastructure of these rectal papillae or rectal pads is well known only in certain insects, including: Dictyoptera (Oschman and Wall, 1969; Noirot and Noirot-Timothee, 1976), Orthoptera (Baccetti, 1962; Peacock, 1979), Isoptera (Noirot and Noirot-Timothee, 1917), Trichoptera (Cianficconi *et al*., 1984; 1985),

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and Lepidoptera (Judy and Gilbert, 1970).

In Dipteran insects, the ultrastructures of rectal papillae have been well-studied in the blow fly *Calliphora erythrocaphala* (Gupta and Berridge, 1966a; 1966b); the fruit fly *Drosophila melanogaster* (Wessing and Eichelberg, 1973); the mosquitoes *Aedes aegypti* (Hopkins, 1967) and *Ephydra riparin* (Eichenberg, 1974); the house fly *Musca domestica* (Flower and Walker, 1979); the olive fruit fly *Dacus oleae* (De Marzo *et al.*, 1978); and the mediterranean fruit fly *Ceratitis capitata* (Dallai *et al.*, 1985). The functions of rectal papillae in these insects have been also demonstrated by Berridge and Gupta (1967) with *Calliphora*, Hopkins (1967) with *Aedes*, and Wessing and Eichelberg (1973) with *Drosophila*.

The morphology of rectal papillae in the male oriental fruit fly *Dacus dorsalis* was preliminary studied with scanning electron microscopy by Lee *et al.* (1990). In this paper, we will describe their ultrastructural organization and compare them with other Dipterans mentioned above.

MATERIALS AND METHODS

Recta of male *Dacus dorsalis* were obtained by the dissection of flies in buffer solution. The fresh recta were photographed under a Wild type M8 microscope.

Rectal papillae were taken from the recta and fixed with 2.5% glutaraldehyde + 0.1 M cacodylate buffer (pH 7.2–7.4 at 6°C for 2 hrs. Specimens used for the scanning microscopic studies were dehydrated with a series of acetone from 50% to absolute. After Critical Point Dryer treatment, specimens were coated with gold with an IB-II Ion Coater. Some specimens were fractured and coated with gold. All specimens were observed with a Hitachi S-450 scanning electron microscope. For the transmission electron microscopic studies, the rectal papillae were washed in cacodylate buffer with 8% sucrose after being fixed in 2.5% glutaraldehyde + 0.1 M cacodylate buffer for 2 hrs. Specimens were post-fixed in 2% osmium tetroxide at 6°C for 2 hrs. After washing with distilled water, specimens were stained with 2.5% uranyl acetate in 50% ethanol for 3 hrs., dehydrated with a series of ethanol concentrations from 50% to 100%, infiltrated in propylene oxide, and finally embedded in Spurr low-viscosity medium. Ultrathin sections were made with Richard Jung Ultracut-E and co-stained with uranyl acetate and lead citrate, then observed with a Ziess 109 and an Hitachi H-7000 TEM.

OBSERVATIONS

General descriptions of the rectal papillae of *Dacus dorsalis*

From previous morphological studies (Lee *et al.*, 1990), the rectal papillae of the male oriental fruit fly, *Dacus dorsalis* are located at the anterior part of the rectum. Four bases of papillae protrude outside the rectum (Fig. 1, PR), while the apical regions (pouches) are embedded within the rectal lumen. Figure 2 shows that the papillae are comprised of a circular base with about 30 segments and a rod-shaped tip. The anatomic structure of the papillae (Fig. 3) is divided in two parts: the cortex (COR) and the medulla (med); between these there is an infundibular space (INF). Seven intercellular spaces (INS) are scattered in the cortical epithelium (Figs. 4 and 5). Each intercellular space contains two or more tracheoles (Tr).

Cortex of the basal region

The cortex of the rectal papillae basal region in *Dacus dorsalis* (Fig. 6) is covered with a thick basement membrane (BM),

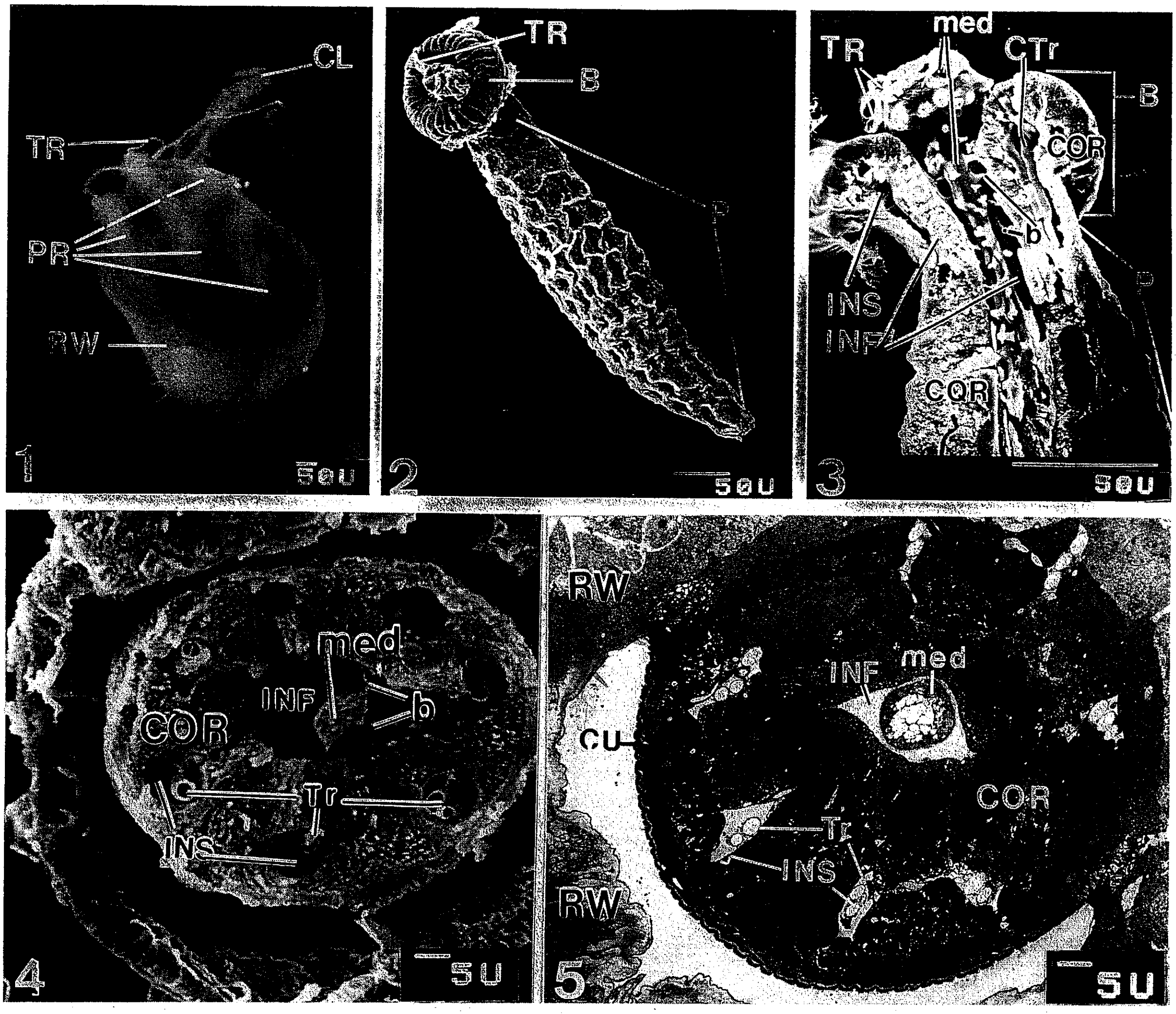


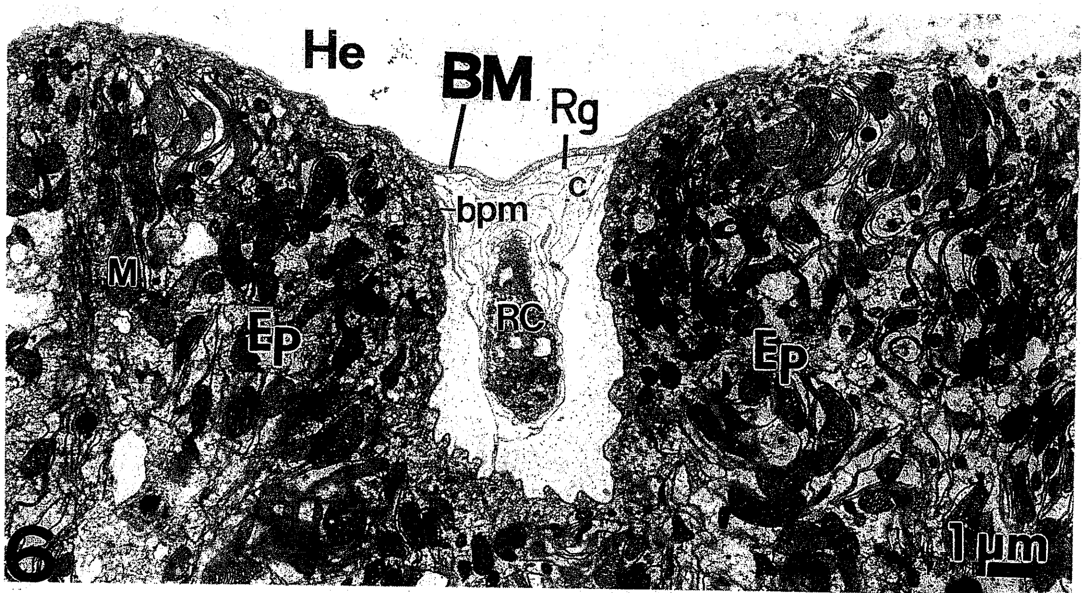
Fig. 1. A light micrograph of morphological structure of a male oriental fruit fly rectum. B: basal region of rectal papillae; PR: apical region of rectal papillae embedded within rectal Lumen; CL: colon; RW: rectal wall; TR: trachea.

Fig. 2. A scanning electron micrograph of rectal papilla. B: basal region; P: apical region; TR: trachea.

Fig. 3. An internal micrograph of rectal papilla with SEM. b: trabecula; B: basal region; COR: cortex; CTr: cortical tracheole; INF: infundibular space; INS: intercellular space; med: medulla; TR: Tracheal branches.

Fig. 4. Transversal fracturing section of rectal papilla with SEM showing the positions of medulla (med), cortex (COR) and infundibular space (INF). Trabeculae (b) across the infundibular space connect medulla and cortex. Seven intercellular spaces (INS) are scattered within the cortical epithelium. Two or three three tracheoles (Tr) are located within each intercellular space.

Fig. 5. Cross section of TEM micrograph showing same structure as Fig. 4. Cuticle (Cu) of papilla appears as an undulating structure surrounding papilla. Medulla (med) appears as a network structure in the middle section. COR: cortex; INF: infundibular space; INS: intercellular space; RW: rectal wall; Tr: tracheole.



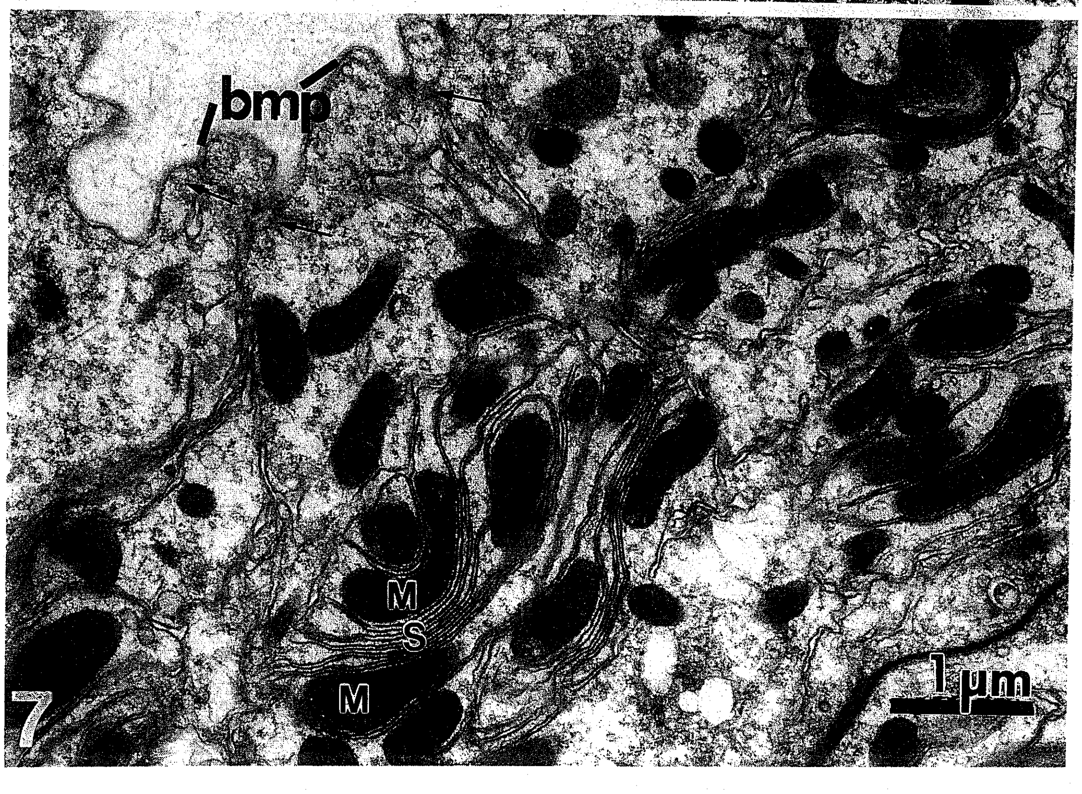


Fig. 6. TEM micrograph of basal region shows a radial cell (RC) between two cortical epithelial cells (Ep) which are incorporated within the basement membrane (BM) covering the basal plasma membrane (bpm) of the cortical epical epithelium. C: connective tissue; He: haemolymph; M: mitochondria; Rg: radial groove.

Fig. 7. Magnification of Fig. 6 shows membranes rising from the basal plasma membrane (bpm) to make membraneous stacks (S) which are associated with mitochondria (M).

and is composed of a single layer of large-sized epithelial cells (Ep). Underneath the basement membrane, a radial cell (RC) surrounded by several connective tissue shealths (C) is located between two cortical epithelial cells. The position of the basement membrane with the incorporated radial cell is the radial groove between two segments shown in the scanning electron micrograph. The cytoplasm of the radial cells provides mitochondria, the endoplasmic reticulum, and the nucleus.

The cortical epithelial cells are surrounded by basal plasma membrane (Fig. 7, bpm). An abundant number of membranes arise from the basal plasmic membrane to form membranous stacks (S). These membranous stacks appear to be intimately associated with the mitochondria (M).

Cortex of the apical region

The cortical epithelial cells of the apical region are also composed of a single layer whose surface is covered with a cuticular intima (called the cuticle in this study (Fig. 8 Cu)) which lines the rest of the rectal wall (Fig. 5, RW). The cuticle of a rectal papilla has an undulating architecture; the apical plasmic membrane under the cuticle is folded into the border of the leaflets (Fig. 8, arrow). These leaflets resemble the profiles of the microvilli. Elsewhere, the cortical epithelial cells contain the endoplasmic reticulum (ER), mitochondria (M), and free ribosome (R). In the connected part of the cell (Fig. 9), many mitochondria (M) are closely associated with the membranous stacks' (S) limited channels. These channels (arrows) open into either the diverticular or branches of the intercellular spaces (Ins).

At the basal part of the cortical epithelial cells, facing the infundibular space, is a basement membrane (Fig. 10, BM) where the plasmic membrane infolds into the cytoplasm; this produces deep infoldings (Bi), or forms a long intercellular sac. Some of these infoldings connect to the membranous stack (S) or the intercellular space. The free ribosomes (R) appear more abundant in the basal part of the cell than the apical part.

The prominent mitochondria (M) of the cortical epithelial cells contain closely-packed, plate-like cristae and a dense matrix. They are intimately associated with membranous stacks (S) (Figs. 10 and 11).

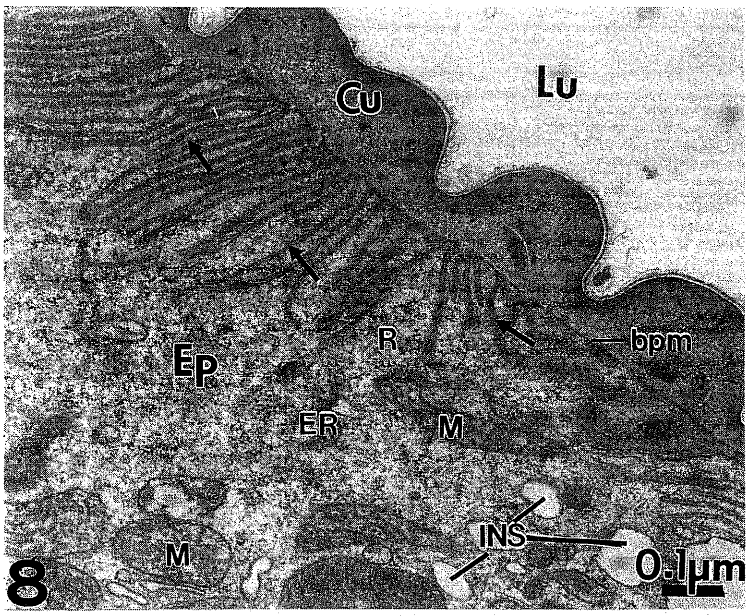
The adjacent cells are separated by the septate junctions (Sj), the tight junction (Tj), and the desmosome (SD) which either extend along the intercellular cleft (Fig. 11, INS), or contact with the membranous stacks (Fig. 12, S). The hemidesmosomes (hd) are always present at the basal part of the cell contact.

Medulla

Within the central area of the papilla, the medulla (Figs. 3 and 4, med) forms a loose structure of cellular strands (Fig. 5, med). The medullary cells (MC) are at the periphery of the medulla and are lined with a basement membrane (BM) which faces the infundibular space (Fig. 13, INF). The large spaces made by the loose network of cellular strands were named by Graham-Smith (1934) as the medullary cavity. They have a prominent nucleus (N); the cytoplasm contains many profiles of mitochondria (M) and cisternae of the endoplasmic reticulum (ER). Some cisternae of the endoplasmic reticulum are swollen to form the network structure.

Connective tissue shealth and trabeculae

The connective tissue shealth or the basement membrane has been previously



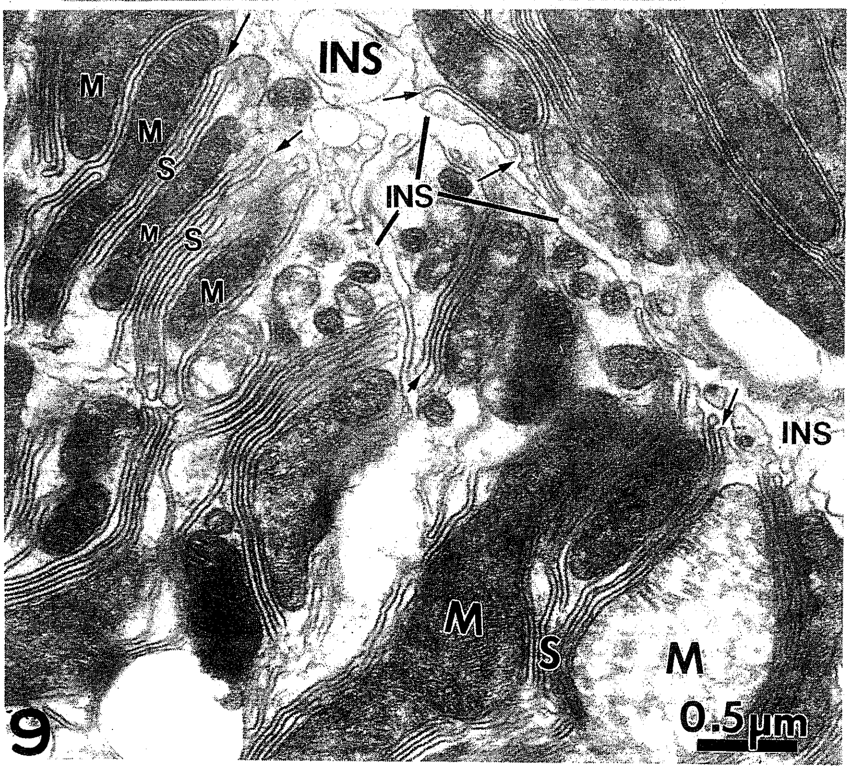


Fig. 8. A small field of the apical part of a cortical epithelial cell (Ep) in the apical region of a papilla. The cuticle (Cu) shows an undulating structure. The basal plasmic membrane (bpm) infolds to form leaflets (arrows). ER: endoplasmic reticulum; INS: intercellular space; Lu: rectal Lumen; M: mitochondria; R: free ribosomes.

Fig. 9. A small field of the lower part of the cortical epithelium shows mitochondrial pumps which are made by membranous stacks (S) associated with mitochondria (M). Membranous stacks (S) open to intercellular spaces (INS) which are highlighted by marks with arrows.

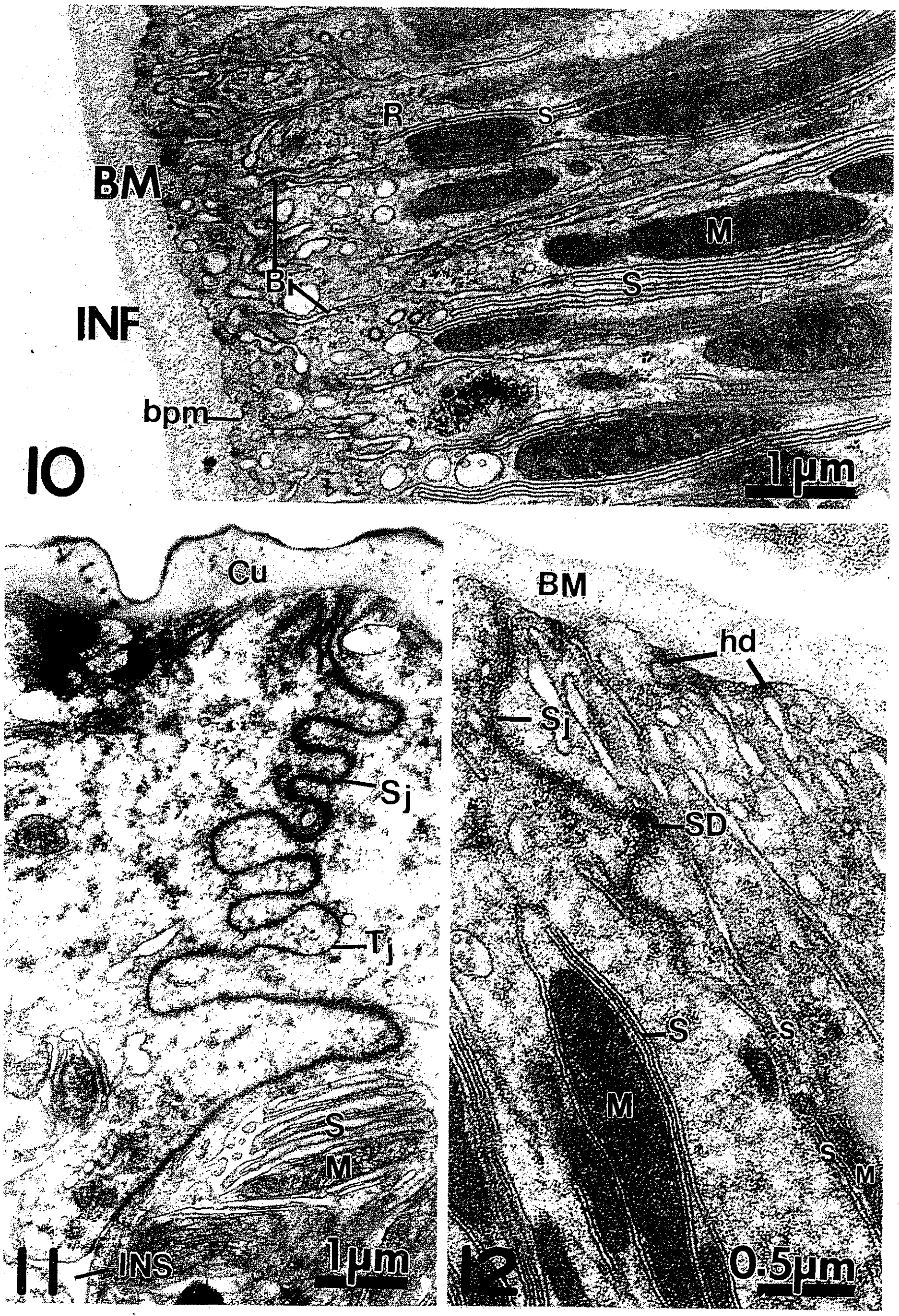


Fig. 10. A small field of the basal part of the cortical epithelium shows the basal plasmic membrane (bpm) infolding into the cytoplasm. Some basal infoldings (Bi) are connected to the membranous stacks (S). BM: basement membrane; INF: infundibular space; M: mitochondria.

Fig. 11. A cross section of the apical part of the cortical epithelium. The septate junction (Sj) and tight junction (Tj) are noted as a cell junction which extends from the basal plasmic membrane (bpm) to the intercellular space (INS). Cu: cuticle.

Fig. 12. A cross section of the basal part of the cortical epithelium. The septate junction (Sj) connects to the membranous stack (S). Hemidesmosome (hd) and septata desmosome (SD) are noted. BM: basement membrane; M: mitochondria.

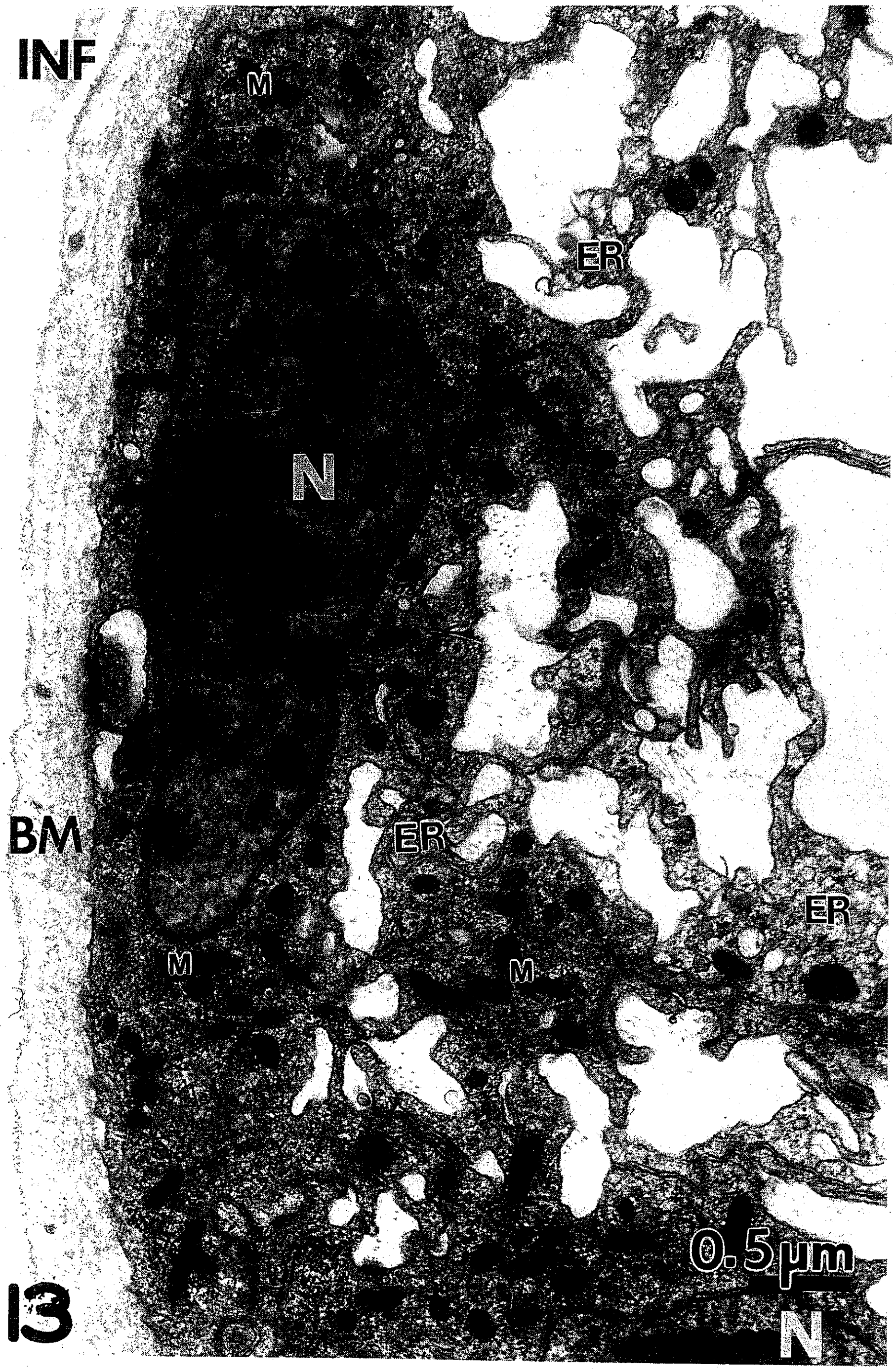
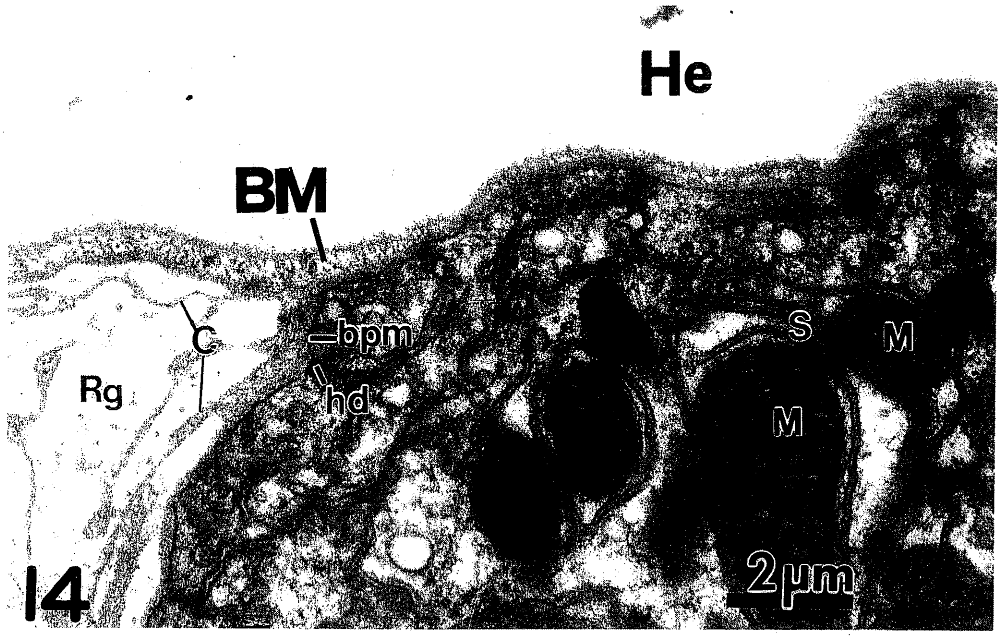


Fig. 13. A TEM micrograph of the medulla. The elongated nucleus (N) of the medullary cell (MC) is located at the periphery of the medulla. Endoplasmic reticula (ER) are swallen to make the central part of the medulla a network structure. BM: basement membrane; INF: infundibular space; M: mitochondria.



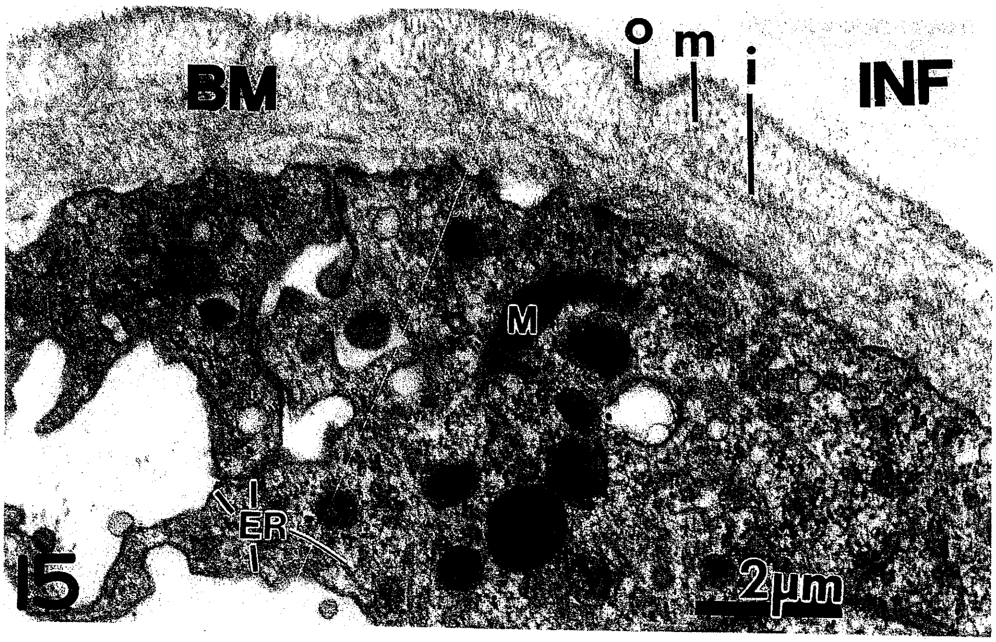
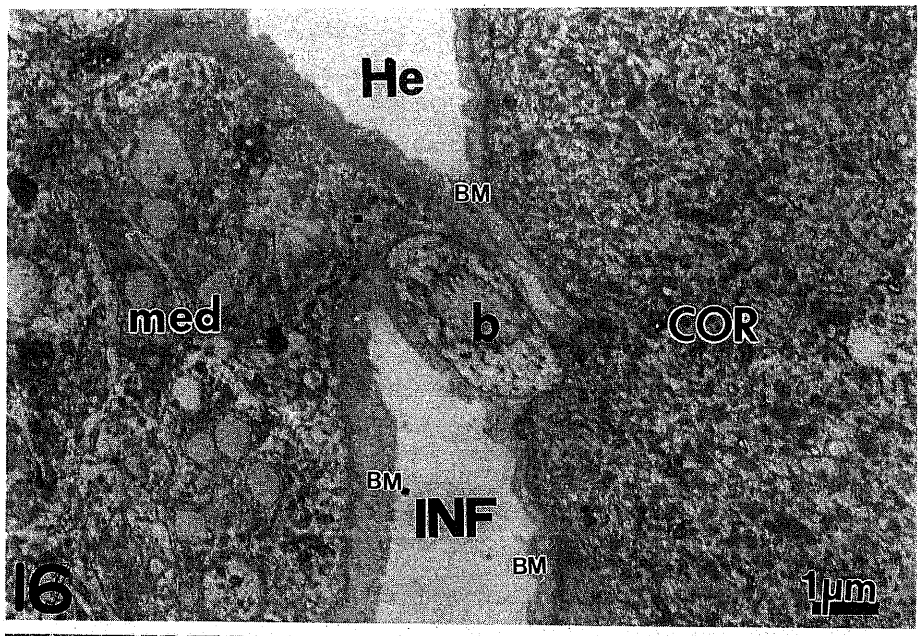


Fig. 14. A small field of the basement membrane (BM) of the basal region cortical epithelium appears as a string-like fibrous structure. bpm: basal plasmic membrane; C: connective tissue; hd: hemidesmosome; He: haemolymph; INS: intercellular Space; Rg: radial groove.

Fig. 15. Basement membrane (BM) of the medulla appears as three layers: a thin and dense outer layer (O), a lamellar inner layer (m). INF: infundibular space.



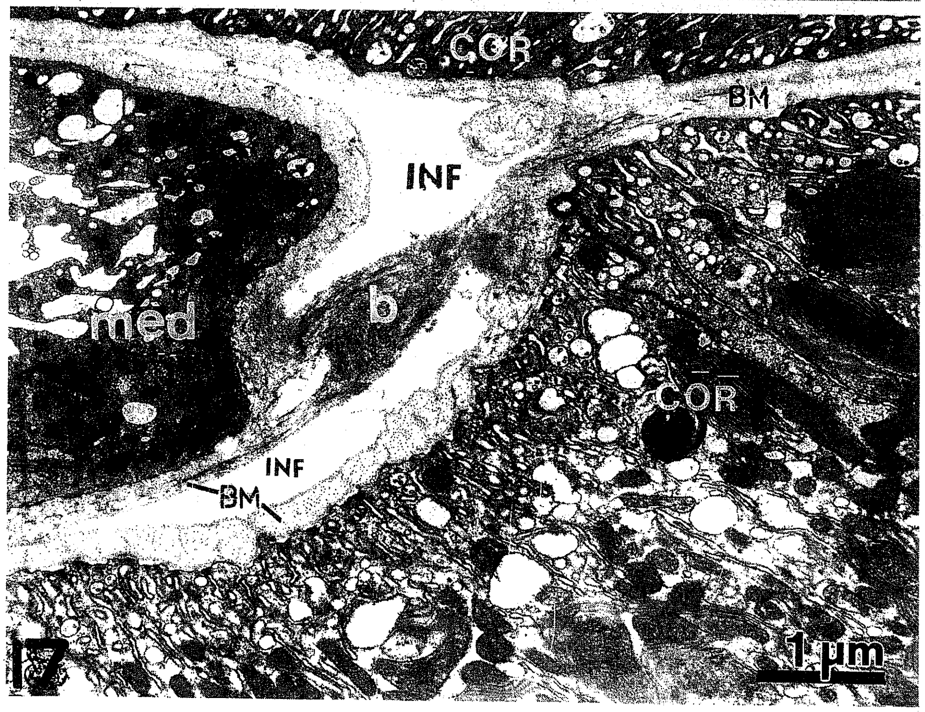


Fig. 16. A longitudinal section of the basal region of a papilla. A trabecula (b) connects the cortex (COR) and medulla (med) appears as an oval shape with its interior containing a collagen cluster and fibrils, and its exterior surrounded by a basement membrane (BM). He: haemolymph; INF: infundibular space.

Fig. 17. A cross section of an apical region papilla. A fibrous trabecule (b) connects the cortex (COR) and medulla (med) across the infundibular space (INF).

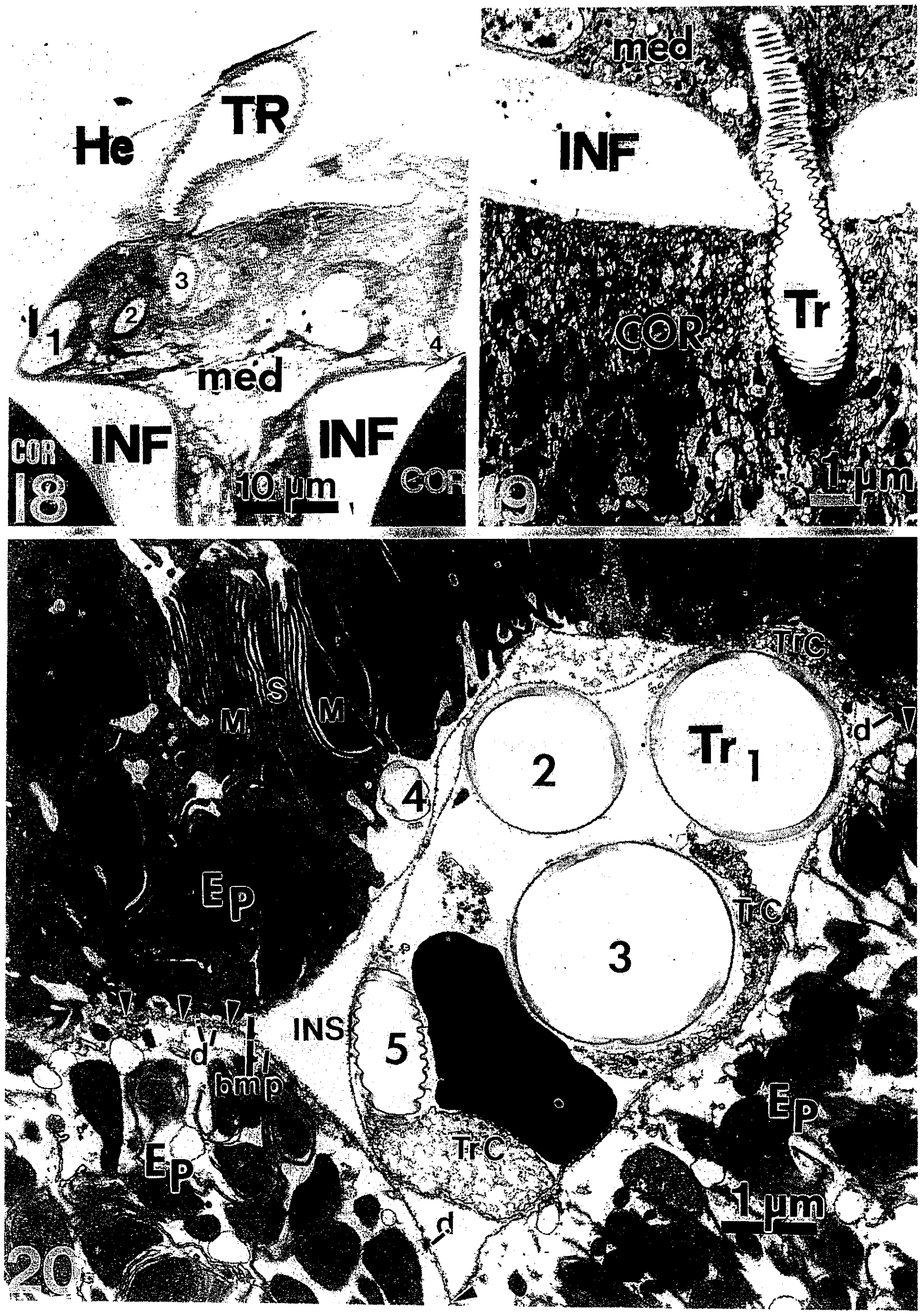


Fig. 18. A low-magnification TEM micrograph of a medulla base (med) shows a trachea (TR) inserted into the base of the medulla. The tracheal branches are numberred 1, 2, 3, and 4; number 4 extends to the cortex (COR). He: haemolymph; INF: infundibular space.

Fig. 19. A small field of the cross section. A tracheole (Tr) crosses the infundibular space (INF) from the medulla (med) to the cortex (COR).

Fig. 20. A cross section from the cortex. Five tracheoles (Tr1, 2, 3, 4, and 5) are located within the intercellular space (INS). The micrograph also shows gaps (arrow) between two neighboring cortical epithelial cells (Ep1, Ep2). TrC: tracheolar cell; d: desmosome.

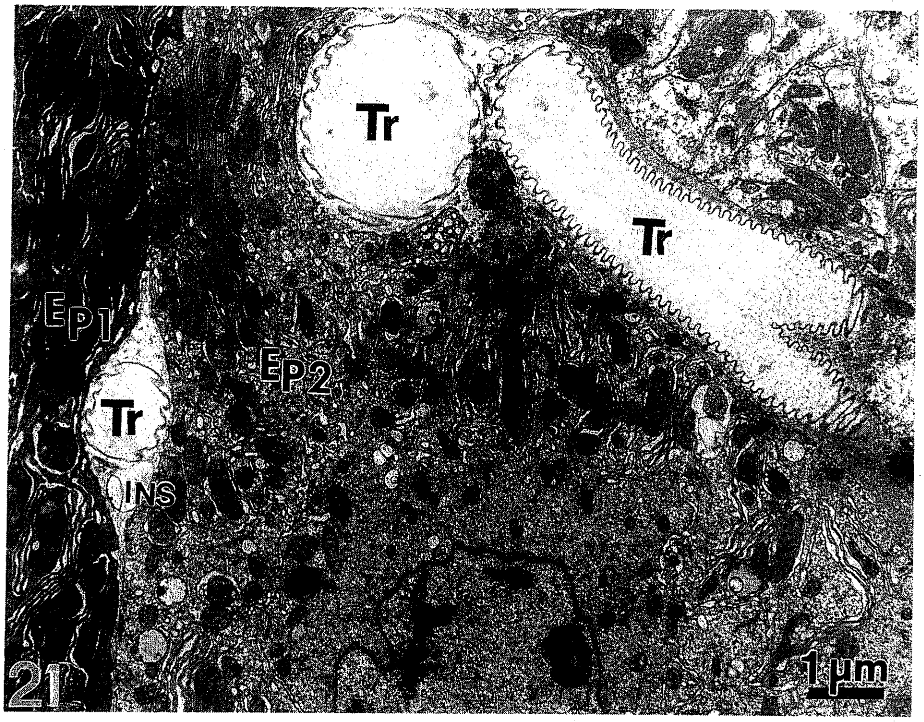


Fig. 21. A small field from the cortical epithelium showing tracheoles (Tr) which have penetrated the cell, plus a tracheole (Tr) which is located within the intercellular space (INS) between two cortical epithelial cells (Ep1, Ep2).

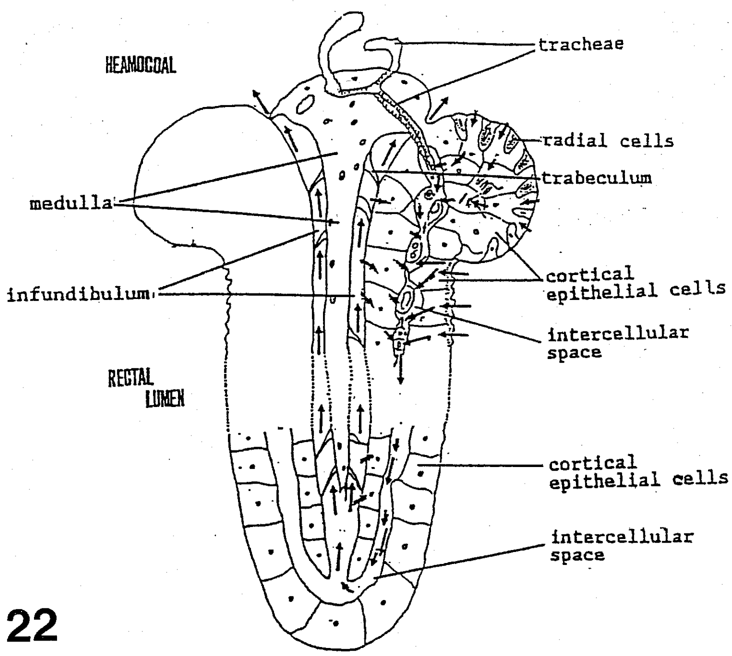


Fig. 22. A diagram showing the pathway of water and ion transport in the rectal papillae of *Dacus dorsalis* Hendel. The long arrows represent water and ion uptake and movement; the short arrows represent the transport of ions (×420).

mentioned, i. e., the basement membrane of the basal region, the basal surface of the cortical epithelium at the apical region, and the basement membrane of the medulla. The basement membrane of the basal region facing the haemolymph appears to be a thick connective tissue string with a fibrous structure (Fig. 14, BM). Within the radial groove (Rg), several connective tissues arise from the sides of the basement membrane (BM) and the basal plasmic membrane (bpm), surrounding and incorporating the radial cell. The basement membrane of the cortical epithelial cell (Ep) facing the infundibular space (INF) at the apical region appears to have a loose amorphous structure which is free of collagen (Figs. 10 and 12, BM). The basement membrane of the medulla has three layers with a sandwitch structure (Fig. 15, BM); the thin outer layer (o) and the lamella-like inner layer (i) enclose a middle layer (m) of collagen-like fibrils.

The trabeculae (b) are bridge-like structures from the medulla to the infundibular space, connecting the medullary and the cortical basement membrane. At the basal region (Fig. 16, b), the oval-shaped trabecula contains a collagen cluster and fibrils on the inside, while on the outside it is surrounded by a basement shealth from the cortex (COR) and the medulla (med). The trabecula in the apical region (Fig. 17, b) is made of compacted fibrous material connecting the two basement membranes (BM) of the cortex and the medulla.

Tracheal system

From SEM (Fig. 3) and TEM (Fig. 18) observations, tracheal (Tr) branches first enter the base of the medulla (med), then cortical branches of tracheae (CTr) extend into the cortical epithelium (COR) and the tracheoles (Tr) across the infundiculum (INF) (Fig. 19); they also go through the intercellular space from the base to the tip of the papilla. There are seven tracheolar clusters with two or more tracheoles within the intercellular space (Fig. 20, Tr, INS). The tracheoles also penetrate into the cytoplasm of the cortical epithelial cell (Fig. 21, Tr).

DISCUSSION

The ultrastructure of rectal papillae in the oriental fruit fly, *Dacus dorsalis* is similar in many aspects to those reported on by Gupta Berridge (1966b) for the blow fly, *Calliphore erythrocephala*; by Eichelberg (1973) for *Drosophila melanogaster*; by De Marzo *et al.* (1978) for *Decus oleae*; by Flower and Walker (1979) for *Musca domestica*; and by Dallai *et al.* (1985) for *Ceratitis capitata*. For example, there are many flattened membranous stacks of intercellular membrane connected to the intercellular space in the cortical epithelium. These flattened membranous stacks are always intimately associated with mitochondria in making ion pumps or mitochondrial pumps. This entire structure is almost identical to those mitochondrial pumps described by Copeland (1964) in the anal papillae of *Aedes* larvae. Both of these pumps occupy most of the cytoplasm of the cortical epithelial cells of rectal papillae in the oriental fly and anal papillae in *Aedes* larvae.

The radial cells located at the basal region of rectal papillae in the oriental fruit fly also occur in the blow fly (Gupta and Berridge, 1966a). The function of these cells is yet unknown. According to its characteristic position, Gupta and Berridge (1966b) suggested that it might play a role in the maintenance of the basement membrane on the surface of the cortex.

Under the cuticle of the apical region of the oriental fruit fly—as in the medi-

terranean fruit fly (Dallai *et al.*, 1985)—the cytoplasmic leaflets of the membrane provide evidence of the role these structures play in active ion transport. Berridge and Gupta (1968) found a strong reaction to Mg^{++}-activated adenosine triphosphatase on the cytoplasmic leaflet in the blow fly. These cytoplasmic leaflets in the rectal papillae of the oriental fruit fly, the blow fly (Gupta and Berridge, 1966b), and the mediterranean fruit fly (Dallai *et al.*, 1985) are similar to the parallel leaflet of anal papillae in *Aedes* larva (Coperand, 1964). However, the function of anal papillae is salt regulation; the cell become tightly folded when larvae are placed in a medium hypotonic to its blood. If the larvae are placed in hypertonic solution, the leaflets show degenerative changes (Sohal and Copeland, 1966).

In the apical region, the plasmic membrane of the cortical epithelium forms various types of cell junctions, i. e., the tight junction, the septata junction, and the desmosome. At the end of a long convoluted area of contact, two plasmic membranes abruptly diverge to form a large intercellular space (Fig. 20, INS) which contains profiles of trachceoles (Tr). These structures seldom occur in the basal region. However, a similar structure has been found in the rectal papillae of the blow fly (Gupta and Berridge, 1966a) and the mediterranean fruit fly (Dallai *et al.*, 1985); however, such a structure does not appear in the rectal pads of adult *Stenophylax permistus* McL. (Cianficconi *et al.*, 1985).

The mechanism of water uptake in the rectal papillae of the blow fly was postulated by Berridge and Gupta (1967); they suggested that solute transport into the mitochondrial membranous stacks produces hyper-osmotic fluid which flows into the intercellular space. Wall and Oschman (1975) stated that water and ions are drawn from the rectal lumen through the cuticle and cytoplasmic leaflets in the apical region of the papillae by local osmosis, and that water and ions can be absorbed from the haemolymph to the cortical epithelial cells in the basal region through the fibrous basement membrane by osmotic gradient. These fluids—both in the basal region and the apical region—flow through the intercellular spaces to the infundibular space. Ions or other solutes are recycled to the epithelium from the infundibular space penetrating the amorphous structural basement membrane in order to contribute to local osmotic gradients during each cycle. Berridge (1970) hypothesized that the water movement gradient in the rectal papillae depends solely on maintaining a high solute concentration in the intercellular spaces. If solutes from sources other than the lumen reach the ion pump, water will flow against an osmotic gradient in the absence of a net flux of solute. Berridge (1970) also stated that with the *Calliphora* fly there are two possible sources for the extra solute in rectal papillae. First, solutes may be recycled within the epithelium as reclal absorbate moves along the infundibular space; the ion—but not the water—could be returned to the cells to be re-used in bringing more water from the lumen. This phenomenon of solute recycling has also been observed in the recta of *Periplaneta* (Oschman and Wall, 1969; Wall and Oschman, 1975). Second, the ion may be recruited from the haemolymph through the surface of the papillar base which faces the haemolymph in order to establish osmotic gradients needed to absorb the water. This situation has been demonstrated in the cryptonephric system of *Tenebrio molitor* (Grimstone *et al.*, 1968).

Trabeculae of rectal papillae in the oriental fruit fly have a different shape

and structure in the basal region from those in the apical region. The structure of trabeculae in the apical region is similar to the trabecular bridge in *Calliphora* papillae (Gupta and Berridge, 1966a), but much thicker. The fibrous materials were presumed by Gupta and Berridge (1966b) as being mucopolysaccharide. Graham-Smith (1934) believed that these trabeculae were perforated with very fine canals ("transinfundibular canals") which allow for the flow of nutritive fluids from the medullary cavity to the "subcellular" cavity. Gupta and Berridge (1966a) also suggusted that trabeculae provide channels for the "flow" of collagen-like fibrils produced in the medulla to the cortical basement membrane. The structure of trabeculae in the basal region of oriental fruit fly papillae differs from that of the blow fly; the former appears oval in shape, and the latter appears to be a thin sheet without any special feature such as the medullary or infundibular valves. Gupta and Berridge (1966a) reported that the function of these valves is to prevent fluid from the haemolymph from penetrating into the infundibular space. Our explanation for the oriental fruit fly is that the fluid only flows from the infundibular space to the haemolymph due to osmotic gradients.

In conclusion, the function of rectal papillae in the oriental fruit fly can be postulated according to their architectural structure as assisting water and ion transport from the rectal lumen to the haemolymph. Water and ions from the rectal lumen are absorbed into the cortical epithelium of papillae in the apical region by means of an osmotic gradient between the cortical cells and the mitochrondrial pumps (the ion pump); in addition, ions in the haemolymph also cross to the cortical epithelium of the basal region through the mitochondrial pump. All water and ions flow into the infundibular space through the intercellular spaces; ions from the infundibular space are reabsorbed and recycled into the cortical epithelium across the basement membrane by the same mitochondrial pump. Finally, nutrient water and ions enter the haemolymph from the infundibular space. The route of the fluid flowing from the rectal lumen to the haemolymph through the rectal papillae of the oriental fruit fly is diagrammed in Fig. 22.

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東方果實蠅 (*Dacus dorsalis* Hendel) 雄蠅之直腸突起微細結構

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本研究係用掃描電子顯微鏡和穿透性電子顯微鏡研究東方果實蠅 (*Dacus dorsalis* Hendel) 雄蠅直腸突起 (Rectal papilla) 之微細結構，該蠅之直腸突起的結構與其他高等雙翅目昆蟲相似。其重要結構包括皮層上皮細胞層 (Cortical epithelium) 和髓部 (Medulla)，兩者間有漏斗溝 (Infundibular space)。在直腸突起基部 (Basal region of papilla)，皮層上層細胞外被有一層纖維結構之基膜 (Fibrous basement membrane)。在端部 (Apical region) 者爲一層表皮層 (Cuticular intima)。皮層上皮細胞內有許多由細胞質膜 (Plasmic membrane) 形成之膜囊 (membranous stacks)，其與粒線體 (Mitochondria) 緊密排列而構成粒線體幫浦 (Mitochondrial pump) 或稱離子幫浦 (Ion pump) 爲直腸內之水份和離子運輸用，皮層上皮細胞基部之基膜爲沒有形態結構 (Amorphous)。細胞質膜內陷 (Infoldings) 與膜囊相接，使漏斗溝內之離子抽回皮層上皮細胞內。皮層上皮細胞間有明顯之細胞間帶 (Intercellular junction) 和小突體 (Desmosome)。許多細胞間空隙 (Intercellular spaces) 插入細胞內，兩或三條微氣管 (Tracheoles) 在較大之細胞空隙內。髓部中間結構呈網狀，周邊有許多髓部細胞核 (Nuclei of medullary cells)，外被有具三層不同結構之基膜。東方果實蠅直腸突起對直腸腔 (Rectal lumen) 內之水份和離子吸收運轉之機制和途徑均討論於原文。